CRITICALLY ASSESSING STOCK ENHANCEMENT: AN INTRODUCTION TO THE MOTE SYMPOSIUM

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ABSTRACT

Stock enhancement represents a potential component of an economically viable and ecologically sound management strategy for many marine fisheries in danger of collapse. Stock enhancement is appealing because of its straightforward logic: by raising large numbers of larvae or juveniles and then releasing them into the marine environment, we can compensate for the enormous natural mortality in these stages and thereby increase the stock size in the late juvenile and early adult stages of the life cycle, which in turn will compensate for the fishing mortality that depleted the stock. Many questions remain, however, about the economic and ecological soundness of this strategy. These questions reach into virtually every area of environmental biology, from population dynamics and genetics to ecosystem processes and resource economics. This first William R. and Lenore Mote Symposium is designed to focus attention on these questions, suggest profitable avenues of research toward the answers, and lead to an increasingly discerning view of when and where in the marine environment stock enhancement is likely to succeed.

Stock enhancement represents a potential component of an economically viable and ecologically sound management strategy for many marine fisheries in danger of collapse. The appeal of stock enhancement rests in its simple premise and its bold promise. The premise is that we can raise large numbers of larvae or juveniles and, by releasing them successfully into the marine environment, compensate for the enormous natural mortality in these stages and thereby increase the stock size in the late juvenile and early adult stages. The promise is that this intervention will compensate for the fishing mortality that created the problem in the first place. The premise appeals to our confidence in understanding natural population processes and our optimism about managing nature successfully. The promise appeals to our reluctance to impose harsher and less popular conservation measures.

Unfortunately, a host of unanswered questions about stock enhancement lurks behind the premise and clouds the promise. These questions extend into virtually every area of environmental biology, from population dynamics and genetics to ecosystem processes and resource economics. Although we have some of the answers for some fisheries, we cannot offer general conclusions about the effectiveness of stock enhancement. That the questions reach so broadly and that the answers are so sparse indicate that this topic is among the richest conceptual areas in fisheries science and thus was an excellent choice for the first William R. and Lenore Mote International Symposium on Fisheries Ecology.

At first encounter, the issues surrounding stock enhancement can appear bewildering. In this paper we organize those issues into a logical sequence derived from the sequence of decisions necessary for any effective stock-management program. We hope that our organization aids those who approach this topic for the first time but also that it reveals

the interrelationships among the individual contributions to the symposium and guides the interested reader to the papers that focus on specific issues of interest.

WHAT IS THE GOAL OF A STOCK-ENHANCEMENT PROGRAM?

Stock-enhancement programs can have one of three general objectives: to replace a stock that is locally extinct, to rebuild a stock that has collapsed as a viable fishery, or to augment a natural population for a "put and take" fishery. Because the three goals will differ in required intensity of husbandry and face different ecological constraints, they will require different tactics and different economic weighing of relative costs and benefits. These problems are addressed explicitly by Grimes (1995) and Blankenship and Leber (1995) and, in this issue, by Wilson et al. and Stoner and Glazer.

How Should a Stock-enhancement Program Be Designed?

The first decision in stock enhancement is the choice of species. As Hilborn, Masuda and Tsukamoto, and Leber et al. discuss in this issue, stock enhancement is likely to be a viable option only for some fisheries. Successful stock enhancement is possible only for species with density-independent mortality in the larval or juvenile stage or, for species with density-dependent mortality in those stages, when the natural densities of larvae or juveniles are very low. Of course, the target stock must be one for which sufficient juvenile habitat is available in the area of the prospective release, as discussed in several papers in this issue (Cooney and Brodeur, Leber et al., Olla et al., Peters et al.). These considerations argue that candidates for stock enhancement should be chosen from among those species for which there is sufficient background information on population dynamic patterns, life histories, and habitat requirements, particularly for the focal lifecycle stages. Although this information does not guarantee success, it would be quixotic to attempt a stock-enhancement program without it.

When a target species has been defined, individuals must be selected for breeding and initial production, and the identity of those individuals is critical. When the goal is to augment or rebuild a local stock, the program should use individuals from that stock. This choice has two virtues. First, it maximizes the likelihood that the released fish are genetically well adapted to local conditions. Second, it minimizes the possibility that the released animals, should they breed with wild individuals, will introduce undesirable alleles or allelic combinations that will initiate undesirable local introgressions. When the goal is to replace an extinct stock, the best tactic is to use individuals from as similar an ecological environment as possible. The support for these recommendations is reviewed in this issue by Conover, Shaklee and Bentzen, Tringali and Bert, and Utter; Moksness et al. discuss the interactions of hatchery and wild stocks from a cost-benefit perspective.

The number of individuals chosen for breeding is as critical as their identity (Allendorf and Ryman, 1987; Ryman et al., 1995; Shaklee and Bentzen, this issue; Tringali and Bert, this issue). Two unfortunate consequences arise from using too few individuals as breeding stock (including too few males, even when many females are used). First, the resultant stock may contain only a very limited subset of the genetic variation in the natural population. This founder effect can increase the frequency of a variety of undesirable

traits in the hatchery stock; when these fish are released into the natural population, these traits will be in a substantially higher frequency than normal, with deleterious consequences due to natural selection on the individuals with those traits. Second, the use of too small a breeding stock risks introducing inbreeding effects. The breeding stock may include closely related individuals, in which case the deleterious effects of inbreeding will be manifested from the beginning. Even if this is not the case, if the released fish numerically overwhelm the natural population, many of the subsequent matings in nature are likely to be between close relatives because the released fish come from a very limited number of parents.

The environments in which the production stock is reared and into which it will be released will be strong determinants of the program's success. The choice of an effective environment requires a firm understanding of larval or juvenile physiology (Tanaka et al., this issue), nutrition (Olla et al., this issue), and parasitology (Kennedy et al., this issue). The parasitology of hatchery fish is especially important and perhaps insufficiently appreciated; husbandry conditions should induce a microbial gut flora that is as similar to the natural one as possible. The most obvious reason is that a proper gut flora will promote survival and growth of the hatchery fish in the natural habitat. A second, equally important reason is to prevent the release of the hatchery stock from introducing pathogens or suboptimal microbial floral elements into the natural population; Utter (this issue) describes this problem.

Two important but subtle considerations affect the construction of an optimal rearing environment. The first is to minimize the possibility that, between initial hatching and final release, the hatchery is selecting for distinct alleles or allelic combinations that would be disadvantageous in the natural environment. If this were to occur, the hatchery fish might fail to survive after release, and those that did survive, if they were to breed with individuals from the natural population, would introduce those genes into the natural population and thereby decrease its average fitness. The papers in this issue by Shaklee and Bentzen and Utter describe some of these effects.

The second subtle consideration involves purely phenotypic patterns in the hatchery fish—that is, whether suitable environmental influences on the development of the fish have been incorporated into the hatchery environment. In this issue, Masuda and Tsukamoto, Olla et al., Tanaka et al., and Thorpe describe in various contexts the rapidly growing body of evidence that environmental conditions experienced at critical ontogenetic stages fashion and constrain the responses of fish throughout their lives. Some of these effects persist long after the environmental stimulus has passed. For example, the thermal regime an individual experiences early in development can affect its response to temperature variation throughout its life (Kinne, 1962; Zamer and Mangum, 1979). Olla et al. review how long the physiological effects of stress can persist in juveniles and how those effects increase the cumulative risk of mortality. The possibility that some physiological responses are constrained by environmental effects on female parents that are transmitted across generations (Mousseau and Dingle, 1991) offers an even more sobering area of concern. Moreover, as Masuda and Tsukamoto and Olla et al. illustrate, many behavior patterns are environmentally induced or otherwise "learned," from feeding behavior to antipredator responses.

How Should the Hatchery Fish Be Released?

Four questions arise about how hatchery stock ought to be released to best effect. First, when in the population dynamic cycle should the release be made? Although the general answer intrinsic to a stock-enhancement program is "at the larval or juvenile stage," there is a more subtle range of possibilities. Several papers in this issue (Leber et al., McEachron et al., Rimmer and Russell, Svåsand) describe the ecological factors involved in the trade-off between a relatively early release from the hatchery (large numbers but smaller individual sizes, probable higher post-release mortality rate) and a later release (fewer numbers but larger sizes, probable lower post-release mortality rate). In this issue, Bannister and Addison, Cooney and Brodeur, and Svåsand describe how a program might employ knowledge of the carrying capacity of the habitat, records of predator densities, or historic records of adult stock size to guide the decision-making process.

Second, when in the growing season and where in the habitat should the hatchery stock be released? Stoner and Glazer (this issue) review both the phenological considerations for an optimal release and the factors involved in selecting the appropriate location for the release. This question can be framed in terms of Cushing's (1990) classic "match-mismatch" hypothesis: the release ought to match the availability of the food required by the released stock and minimize their match to the timing and location of maximal predation pressure.

Third, how many fish should be released? Although it is tempting to answer, "as many as we raised," there is evidence that the correct answer is an optimal rather than a maximal number. As Masuda and Tsukamoto and Stoner and Glazer point out in this issue, the immediate increase in local prey density created by the release may lead to a local increase in predation pressure by attracting predators. Cooney and Brodeur, Masuda and Tsukamoto, and Svåsand also describe how a high density of newly released individuals could create a local decrease in food availability and lead in turn to slower growth of the released stock, longer periods at smaller, vulnerable size classes, and increased susceptibility to even normal per capita predation pressure. Both scenarios describe a local elevation in density-dependent mortality rates that can be created by release of too many individuals. Yet even without a local increase in mortality rates, the higher densities may lead to density-dependent changes in the life history of the fish that produce maturation at smaller sizes and lower per capita reproductive output, offsetting any net gain in population numbers from the stock-enhancement program; Masuda and Tsukamoto and Thorpe (this issue) offer an illustration of this scenario.

Fourth, given all of these considerations, what are the economic costs and benefits of different release points? The costs of retaining hatchery stock until the ecologically optimal release age may be unacceptably high, in which case the optimal release will be a joint function of ecological and economic considerations. The papers in this issue by Heppell and Crowder, Leber et al., and Wilson et al. touch upon various facets of this problem.

WHAT ARE THE ENVIRONMENTAL EFFECTS OF STOCK ENHANCEMENT?

Stock enhancement can affect the environment in two ways. The first is the cumulative effect of the hatchery itself on its surrounding environment. The biomass concentrated in hatcheries creates a considerable amount of organic waste, the release of which can create a variety of problems stemming from the eutrophication of the environment. The costs of treating the waste to preclude those problems must be factored into any cost-benefit evaluation of the enhancement program. Although none of the papers in this issue address this problem explicitly, it is an important consideration; the list of examples where intensive aquaculture has led to local environmental deterioration has grown markedly in recent years (Pringle et al., 1993; Axler et al., 1996; Holden, 1996).

The second group of potential effects includes those on the species in the community and ecosystem in which the fishery is embedded. The increased numbers of individuals will have an immediate impact on their food resources; as Grimes (1995), Cooney and Brodeur (this issue), and Masuda and Tsukamoto (this issue) illustrate, other species that exploit those resources can be affected. The connections in the food web may cause effects to resonate even further, and sufficiently strong initial impacts may themselves create new ecological dilemmas. In the long term, such effects could cycle back to the stock at which they began.

DOES STOCK ENHANCEMENT WORK?

The roster of problems besetting stock enhancement might dissuade anyone from attempting such a program, but if stock enhancement can work, and work at an acceptable economic cost, then those problems become "opportunities" and not impediments. However, as reflected in this issue, the divergent points of view between Hilborn and Moksness et al. on the one hand and McEachron et al. and Rimmer and Russell on the other, it is not clear to all that stock enhancement works. This disagreement arises because stock enhancement is not a fully experimental discipline. The effects of a stock enhancement program will probably be observed in the context of other changes in management strategies or other ecological changes in the system; it may be difficult even to determine which effects are due to stock enhancement. For example, Cooney and Brodeur and Coronado and Hilborn show how changes in ocean conditions can overwhelm any potential effect of the release on the natural stock size.

The criteria for "success" will vary from one program to another as the goals of the program vary. As Hilborn (this issue) suggests, the judgment of "success" will be a complex function of ecological, economic, philanthropic, political, sociological, and perhaps even religious factors. At one extreme, Heppell and Crowder's case study illustrates a circumstance in which the recapture of only two released individuals is judged sufficient by some to indicate success. At the other, Svåsand's history of the Norwegian cod enhancement programs and Bannister and Addison's discussion of those for the north Atlantic lobster illustrate how ecological, economic, and sociological issues, from cod population sizes to job creation, affect how a program's success is perceived.

The "acceptable economic cost" is more subtle yet. Not only must these conclusions be based on a variety of assumptions, but those assumptions will be different for different economic situations. For example, as Moksness points out, salmon ranching is unlikely to

be profitable and requires government subsidy; this subsidy is regarded as funding well spent for a variety of reasons, a judgment that might turn differently in different political climates. The cost of environmental effects might not be regarded as critical in some areas where those effects are not of concern. In more developed areas, these effects may be of great concern and the costs of absorbing or mitigating them might be so large as to render a stock-enhancement program virtually impossible.

CONCLUSION

The papers in this issue represent the product of three days of presentations, discussions, and arguments over all of these facets of marine stock enhancement. November 21–23, 1996, over 60 scientists gathered at the Mote Marine Laboratory in Sarasota, Florida, USA, to assess the issues we have outlined in this introductory treatment. The goals of this symposium, which was sponsored by the William R. and Lenore Mote Eminent Scholar Chair at Florida State University, were to focus attention on these questions, to suggest profitable avenues of research toward their answers, and to lead to an increasingly sophisticated view of when and where in the marine environment stock enhancement is likely to represent an effective component of fisheries management. The divergent viewpoints expressed in many of these contributions, along with the tone and content of the round-table discussion session that followed the oral presentations, illustrate how far we are from a scientific consensus. On the other hand, the contributions themselves illustrate how much we have learned and how important further work will be.

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